PATCH EXPLOITATION AND DEFENCE
IN THE EGG PARASITOID
Trissolcus basalis WOLLASTON
(HYMENOPTERA: SCELIONIDAE)

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# Table of Contents

Summary ...................................................................................................................... vii
Declaration ................................................................................................................ x
Acknowledgements ................................................................................................... xi
List of Figures .............................................................................................................. xvi
List of Tables ............................................................................................................. xx

Chapter 1: Introduction .............................................................................................. 1
1.1 Behavioural ecology & foraging theory ............................................................... 1
1.2 Host acceptance: superparasitism & host discrimination ................................. 2
1.3 Competition: interference & patch defence ....................................................... 5
1.4 Patch-leaving ...................................................................................................... 7
1.5 General biology of *Trissolcus basalis* ................................................................. 9
1.6 Aims of the project .............................................................................................. 10

Chapter 2: Field Ecology ......................................................................................... 13
2.1 Introduction ......................................................................................................... 13
2.2 Methods ............................................................................................................. 13
2.3 Results .............................................................................................................. 16
   2.3.1 Host plants, hosts and parasitoids ............................................................... 16
   2.3.2 Host emergence and mortality ................................................................... 18
   2.3.3 Parasitoid egg load .................................................................................... 21
   2.3.4 Parasitoid patch exploitation and competition .......................................... 21
2.4 Discussion ......................................................................................................... 27
# Chapter 3: Oviposition and Patch Exploitation

3.1 Introduction .................................................................................................... 29

3.2 Methods ......................................................................................................... 31

3.2.1 Rearing ....................................................................................................... 31

3.2.2 Experiments ............................................................................................... 31

3.2.3 Behavioural categories ............................................................................. 33

3.2.4 Data analysis .............................................................................................. 34

3.3 Results .......................................................................................................... 36

3.3.1 Egg maturation ......................................................................................... 36

3.3.2 Discussion of behavioural categories ......................................................... 36

3.3.2.1 Host examination, probing and drilling .................................................. 36

3.3.2.2 Oviposition and host marking ................................................................. 38

3.3.2.3 Patch-leaving ......................................................................................... 42

3.3.2.4 Patch defence ......................................................................................... 42

3.3.3 Time inhomogeneity and deviations from exponentiality ....................... 43

3.3.3.1 *Walk-antennate host* ........................................................................... 46

3.3.3.2 *Turn* .................................................................................................... 49

3.3.3.3 *Probe, Pump and Rock* ................................................................. 52

3.3.3.4 *Mark* .................................................................................................. 55

3.3.3.5 *Walk-antennate substrate* ............................................................... 57

3.3.3.6 Stationary and patrol .......................................................................... 59

3.3.4 Sequential dependencies .......................................................................... 61

3.3.5 Patch-leaving times .................................................................................. 64

3.4 Discussion ..................................................................................................... 56

# Chapter 4: The Pay-off from Superparasitism

4.1 Introduction .................................................................................................... 72

4.2 Methods ......................................................................................................... 74

4.2.1 Identification of genetic marker ............................................................... 74

4.2.2 Species identity ......................................................................................... 75

4.2.3 Pay-off experiment ................................................................................... 75

4.2.4 Data analysis ............................................................................................. 76

4.3 Results .......................................................................................................... 78

4.4 Discussion ..................................................................................................... 82
Chapter 7: Contest Outcomes .......................................................140

7.1 Introduction ........................................................................140
7.2 Methods ...........................................................................142
7.3 Results .............................................................................145
7.4 Discussion .........................................................................148

Chapter 8: Host Discrimination ...............................................152

8.1 Introduction ........................................................................152
8.2 Methods ...........................................................................154
  8.2.1 Monte-carlo simulations .............................................155
8.3 Results .............................................................................163
  8.3.1 Self-discrimination .....................................................163
  8.3.2 Conspecific-discrimination ........................................163
8.4 Discussion ..........................................................................165

Chapter 9: General Discussion .................................................168

9.1 Project overview ..............................................................168
9.2 Future research ...............................................................171

Appendix 1: Publications ........................................................174

References ................................................................................175
Summary

*Trissolcus basalis* (Wollaston) (Hymenoptera: Scelionidae) is a solitary endoparasitoid of the eggs of many pentatomid bugs (Hemiptera: Pentatomidae), and has been widely used as a biocontrol agent. As with many other quasi-gregarious scelionids, it aggressively defends host patches, an issue in parasitoid behavioural ecology that remains largely unexplored. The work presented in this thesis was aimed at investigating various aspects of patch defence in *T. basalis*.

In the Adelaide region of South Australia, the most abundant host of *T. basalis* is the native horeshound bug, *Agonoscelis rufula* (Fabricius). Over two seasons in the period of peak activity in spring and early summer, aspects of the ecology of this host-parasitoid system were studied and competition among parasitoids for access to host patches was observed. Levels of competition varied widely between seasons, and the behavioural responses of wasps reflected the importance of competition in their foraging ecology.

The temporal structure of oviposition and patch exploitation behaviour by wasps alone on a patch was studied in the laboratory and major departures from the basic assumptions of a first-order Markov chain were detected. Biological interpretations of these departures are given, and the general sequence of behaviour is summarised. Of particular significance was the occurrence of elements of agonistic behaviour, despite the absence of competitors.

The time-dependence of the payoff from superparasitism was examined in an experiment using two strains of *T. basalis* that were distinguished using a genetic marker. Results showed that for several hours after oviposition by the first wasp, the payoff from superparasitism was greater than 50%. Evidence points to this being due to a shift in sex ratio by the superparasitising female toward faster-developing male progeny, an hypothesis consistent with local mate competition theory.

Agonistic behaviour by wasps in pairwise contests was studied in the laboratory by varying the patch size and the time at which the second wasp was released onto the patch. The
resulting data were used to: 1) analyse the time structure of behaviour and develop the conceptual basis for game-theoretic models of patch defence; 2) investigate the factors stimulating the onset of aggression; 3) identify the factors determining the outcomes of agonistic interactions; and 4) test for the ability of conspecific host discrimination.

Over the course of patch contests, agonistic roles emerged in which one individual, the 'resident' monopolised access to the patch, while the 'intruder' alternated between waiting nearby and attempting to return to exploit the patch. The time structure of contests was generally characterised by three periods, each defined by abrupt changes in behaviour by one or both individuals: 1) oviposition period - oviposition by both individuals with no aggression; 2) contest period - aggression and resolution of agonistic roles, ending when one individual (usually the resident) left the patch; and 3) superparasitism period - return of the intruder to the patch and superparasitism. Within these periods, the statistical properties of individual behaviours of resident and intruder, and the overall sequence of contest behaviour were summarised. A key outcome of this analysis was the identification of a "waiting game" toward the end of the contest period, which forms the basis for an evolutionary game theory model of patch defence, in ongoing collaborative work.

The factors stimulating the initial onset of aggression were studied using survival analysis. Survivor functions for the time until onset of aggression from different release-time treatments suggested that the tendency to begin fighting was influenced by variations in patch-size and experience on the patch. The effects of experience were further investigated using the Cox proportional hazards model, which showed the decision to begin fighting was influenced primarily by the number of offspring invested in the patch, the rate of encounter with the opponent, and the rate of encounter with unparasitised hosts.

Determinants of the incidence and outcomes of subsequent agonistic encounters were studied using logistic regression. Contest outcomes were not based on a size advantage, but the probabilities of initiating and then winning an encounter were influenced by a number of other factors: patch-size, the number of offspring invested in the patch, the number of
encounters previously lost, and most importantly, the outcome of the previous encounter, \textit{i.e.}, residency status. The typically rapid and uncontested resolution of agonistic encounters in favour of the resident is interpreted as the result of resource-correlated asymmetries inherent in patch contests.

The abilities of self- and conspecific- host discrimination were tested using a Monte-Carlo simulation model that could test for different possible mechanisms of discrimination. The period in which the intruder returned to superparasitise was used to test for conspecific-discrimination, as theory predicts it should provide a clear fitness advantage in this situation. Results showed that self-discrimination was highly efficient, but that conspecific-discrimination was not occurring. However, wasps could still discriminate against hosts they had parasitised in the current bout of oviposition, possibly using volatiles associated with host fluids issuing from the wound made during oviposition.

The study of patch defence draws together important areas of research in parasitoid behavioural ecology, including the theories of adaptive superparasitism, sex ratio decisions, foraging behaviour and contest resolution, and provides a number of opportunities for stimulating future research.